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The Perissodactyl Hallux

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The earliest perissodactyls first appear in the fossil record with a tridactyl pes, already having lost the first and fifth toes. The purpose of the present paper is to describe what appears to be a remnant of the first metatarsal in living and fossil tapiroids and rhinocerotoids.

This study was carried out during my tenure of a National Science Foundation Postdoctoral Fellowship in the Department of Vertebrate Paleontology of the American Museum of Natural History. I wish to thank Dr. Richard G. Van Gelder, Chairman and Associate Curator, Department of Mammalogy of the American Museum of Natural History, for help in obtaining a tapir foot for dissection.

The names of institutions are abbreviated as follows:

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History
A.M.N.H.:M., Department of Mammalogy, the American Museum of Natural History
M.C.Z., Museum of Comparative Zoölogy at Harvard College

DESCRIPTION

During a recent study of tapir osteology, I noticed a small, consistently present tarsal bone that apparently had no homologue in the foot of other living perissodactyls. In posterior (plantar) aspect it is flat and roughly rectangular to oval; anteriorly (dorsal view) the lateral half pro-

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jects forward, terminating in an oval articular facet. This bone articulates medially with the laterodistal edge of the entocuneiform and anteriorly with a facet protruding posteriorly from the head of metatarsal III and, in one species, metatarsal IV (see fig. 1). In the New World species of *Tapirus* (*T. bairdii*, *T. terrestris*, and *T. pinchaque*) the entocuneiform facet is short, convex, and not clearly delimited. In the Asiatic species (*T. indicus*) this facet is planoconcave, much larger and better defined, with a raised border and variably developed rough bone patches in the center. This latter feature is interpreted as indicating incipient fusion with the entocuneiform. In the New World species the anterior articulation is confined to metatarsal III. In *T. indicus* it is expanded laterally onto a narrow portion of metatarsal IV.

Dissection of a fresh foot of *Tapirus indicus* showed the above-described bone to be firmly bound by strong tarsal ligaments to the entocuneiform and the posterior process of the cuboid; ligaments also extend to the heads of the three metatarsals. Two powerful deep flexors, the contrahentes, which insert on the proximal phalanges of metatarsals II and IV, take origin from the anterodistal surface of this bone (see fig. 1A).

INTERPRETATION

A consideration of the tarsal structure and musculature suggests two possible functional interpretations. First, in bridging the gap between the entocuneiform and metatarsal III and being tightly bound in by tarsal ligaments, the bone under consideration acts as a strut to brace the tarsus. Second, it provides attachment for the contrahentes. Because it is situated posterior to the insertion of those flexors, it gives a small horizontal component to their pull during contraction, thereby increasing mechanical efficiency.

As no obvious homologue of the above-described bone occurs in the tarsus of recent rhinoceroses or horses, the first explanation that came to mind was that it might be an independently developed sesamoid. However, an examination of the foot of the early Eocene condylarth *Phenacodus* (morphologically representative of the ancestral perissodactyl) suggested another interpretation. *Phenacodus* has a pentadactyl pes, with a flat, vertically elongate entocuneiform articulating distally with the short first metatarsal (see fig. 2). Evolution from this type of foot to that seen in the earliest perissodactyls involved, among other changes, reduction and loss of the first and fifth toes and rotation of the long axis of the entocuneiform to a more horizontal position (compare entocuneiforms in figs. 1 and 2). With the first metatarsal reduced to a vestige, rotation of the entocuneiform would swing it (metatarsal I)

laterad to a position behind metatarsal III. Thus the bone described in the preceeding section seems to be the reoriented vestige of metatarsal I. Such a hypothesis is simpler and more probable than the first mentioned, which requires the appearance of a new bone.

The reason for the rotation of the entocuneiform and lateral displacement of the vestigial metatarsal I in the transition from condylarth to

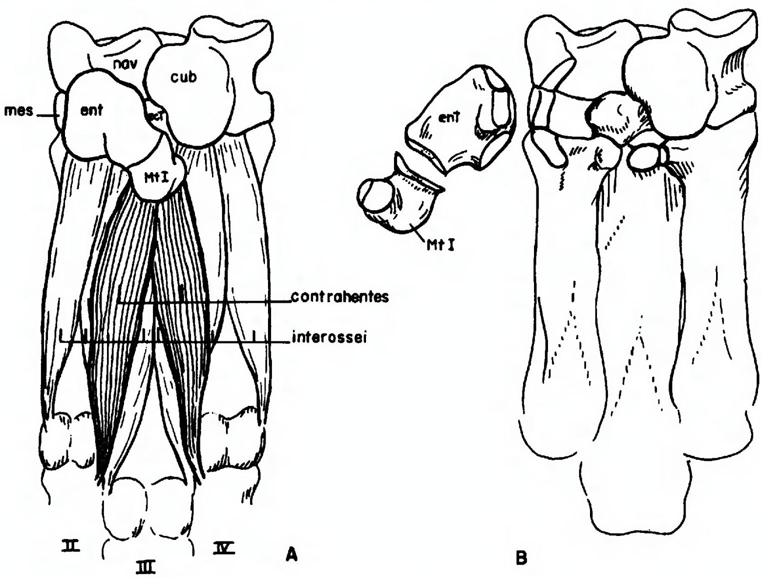

FIG. 1. Plantar (posterior) view of right hind foot of *Tapirus indicus,* showing distal tarsals and metatarsals. A. Deep flexor musculature. B. Musculature removed, and entocuneiform and metatarsal I turned over to show articular facets. × ½.
Abbreviations: cub, cuboid; ect, ectocuneiform; ent, entocuneiform; mes, mesocuneiform; Mt I, metatarsal I; nav, navicular.

perissodactyl apparently is connected with the concomitant reduction of the large, posteriorly projecting process of the ectocuneiform of *Phenacodus.* In condylarths this process probably served as attachment area for the contrahentes and possibly also the interossei of metatarsal II. With reduction of the ectocuneiform process, these deep flexors shifted origin to the laterally displaced entocuneiform and vestigial metatarsal I. Metatarsal I, having shifted to a position behind metatarsal III, was well suited to act as a brace for the tarsus.

THE FOSSIL RECORD

The hypothesis suggested above is supported by a brief survey of fos-

sil perissodactyl tarsi. A vestigial first metatarsal is rarely found in fossil specimens, but its presence may be deduced from articular facets on the back of metatarsal III and on the laterodistal edge of the entocuneiform.

TAPIROIDEA: Metatarsal I is not preserved in any specimen known to me of the oldest (earliest Eocene) tapiroid *Homogalax*, but its presence is indicated by a prominent facet on the anterior face of the laterodistal corner of an entocuneiform in A.M.N.H. No. 15810. In *Heptodon*, a middle

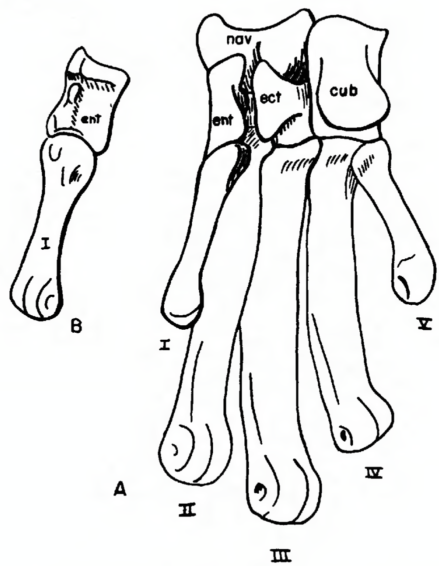

FIG. 2. A. Plantar view of right hind foot of *Phenacodus copei* (A.M.N.H. No. 4378), showing distal tarsals and metatarsals. B. Lateral view of the entocuneiform and metatarsal I. × 1.

Abbreviations: cub, cuboid; ect, ectocuneiform; ent, entocuneiform; nav, navicular.

to late early Eocene tapiroid, metatarsal I is preserved (see fig. 3A). In shape it roughly resembles metatarsal I in *Tapirus*, but no distinct articular facet was developed at the entocuneiform contact. In fact, from the entocuneiform alone, the presence of metatarsal I would not have been suspected. The entocuneiform is somewhat rounder and less laterally extended in *Heptodon* than in *Homogalax* or *Tapirus*.

In *Helaletes*, a middle Eocene descendant of *Heptodon*, metatarsal I (seen in A.M.N.H. No. 11658) is flatter and more extended distally, resembling the shape of metatarsal I in *Colodon* (described below). The entocuneiform facet, however, is convex and poorly defined, as in *Heptodon*.

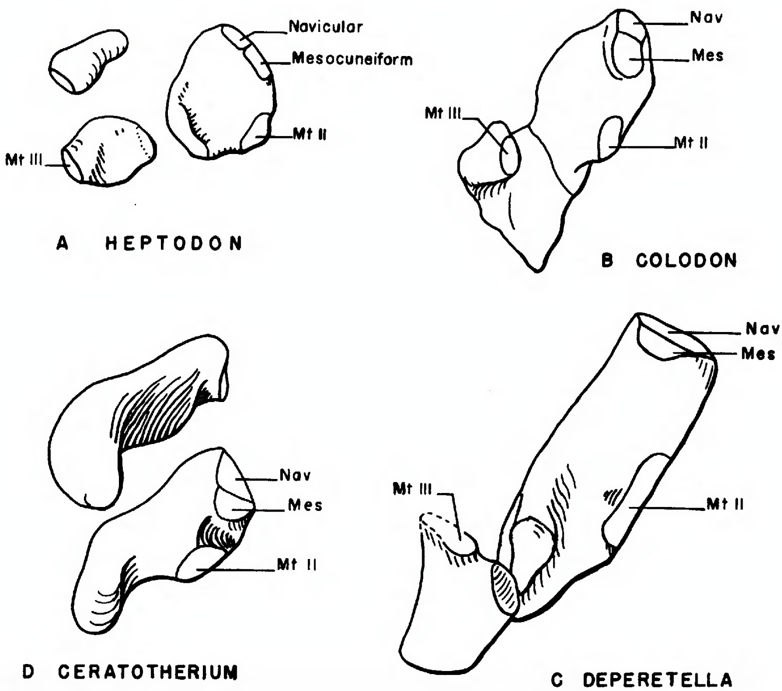

FIG. 3. Tapiroid and rhinocerotoid entocuneiforms and first metatarsals. A. *Heptodon posticus* (M.C.Z. No. 17670), front view, with proximal view of metatarsal I. × 1. B. *Colodon occidentalis* (A.M.N.H. No. 10751), front view. × 1. C. *Deperetella cristata* (composite from A.M.N.H. Nos. 20301 and 20329), front view. × 1. D. *Ceratotherium simum* (A.M.N.H.:M. No. 51862), front and proximal views. × ½.

Abbreviations: Mes, facet for mesocuneiform; Mt II, facet for second metatarsal; Mt III, facet for third metatarsal; Nav, facet for navicular.

In *Colodon,* a late Eocene and Oligocene cursorial descendant of *Helaletes,* two major advances in metatarsal I are evident (see fig. 3B). First, it is diamond-shaped, having been greatly lengthened distally, a fact that provides a larger area for attachment of the contrahentes. The posterior surface of the lateral corner (behind the prominence bearing the articular facet for metatarsal III) is also somewhat extended posterolaterally, probably to give better attachment for the ligaments binding metatarsal I to the cuboid. Second, metatarsal I is firmly fused to the entocuneiform. The suture is still plainly visible, but fusion is complete along the entire contact. This would strengthen metatarsal I both as a brace for the tarsus and as a strut for flexor muscle attachment. These modifications are probably correlated with other changes noted in *Colodon,* such as extreme

lengthening of the distal limb segments, which indicate specialization for cursorial locomotion.

Early Tertiary tapiroids in Asia include two indigenous stocks, both of which preserve an independent vestige of metatarsal I. In the late Eocene genus *Schlosseria* (A.M.N.H. No. 20241), it resembles metatarsal I of *Helaletes*. In another late Eocene tapiroid, *Deperetella,* which exhibits cursorial specializations, the entocuneiform and metatarsal I are still further modified (see fig. 3C). The entocuneiform is roughly rectangular and very elongate, with the lateral end greatly extended distally. This correlates with the extreme elongation of the metatarsals in *Deperetella*. The posterior surface of the laterodistal end of the entocuneiform is raised into a rough oval eminence, perhaps for attachment of the metatarsal II interossei. The vestige of metatarsal I is also lengthened distally, as in *Colodon*, but is somewhat broader than in that genus. A partially broken facet for metatarsal III indicates that, besides serving for muscle attachment, metatarsal I also braced the tarsus.

No tarsi of the European middle to late Eocene tapiroid *Lophiodon* were available for examination, but, according to Depéret (1903, p. 35), the entocuneiform was lost in that genus. Depéret's illustrations (pl. 4, fig. 8) show the navicular to be too narrow to cover even the mesocuneiform completely; it is unlikely therefore that this form had an entocuneiform.

RHINOCEROTOIDEA: In *Hyrachyus,* a middle Eocene descendant of *Heptodon* at present classified as a rhinocerotoid, metatarsal I of A.M.N.H. No. 12675 resembles the first metatarsal in *Heptodon,* while in A.M.N.H. No. 12665 it is slightly longer distally.

Hyracodon, a specialized Oligocene cursorial rhinocerotoid, exhibits an entocuneiform and metatarsal I similar to those of *Colodon,* except that the suture between them is no longer visible and metatarsal I is somewhat smaller. The entocuneiform and metatarsal I were described by Scott (*in* Scott and Jepsen, 1941, pp. 770, 840) as a single bone—an entocuneiform with a peculiar distal process.

In recent rhinoceroses no separate vestige of metatarsal I is present. The entocuneiform is a thick, oval bone, with a club-like process extending almost at a right angle from the lateral end (see fig. 3D). In view of the morphological series described above, including all stages from an independent metatarsal I to one fused to the entocuneiform, it seems likely that the process at the end of the entocuneiform in recent rhinoceroses is actually the fused remnant of the first metatarsal. It does not abut against metatarsal III and thus does not brace the tarsus, but instead apparently serves solely for muscle attachment.

CHALICOTHERIOIDEA: The oldest known chalicotherioid tarsi are those

of the late Eocene North American *Eomoropus amarorum* (A.M.N.H. No. 5096) and Asiatic *Grangeria gobiensis* (A.M.N.H. No. 26655). In both specimens the entocuneiform is present, but there is no trace of the first metatarsal. However, broad facets on the distal ends of the flat rectangular entocuneiforms suggest that metatarsal I was present in life in both genera. Such a suggestion is supported by the presence of a facet on the back of the head of metatarsal III in *Eomoropus* and possibly one on metatarsal IV in *Grangeria*. In the larger later chalicotheres the entocuneiform is lost.

BRONTOTHERIOIDEA: Entocuneiforms of the primitive middle Eocene titanothere *Palaeosyops* (A.M.N.H. Nos. 1589 and 11682) are shaped approximately like those of *Heptodon* and exhibit no laterodistal facet for metatarsal I. In no specimen examined by me was metatarsal III sufficiently well preserved to show whether or not a posterior facet for metatarsal I had been present. In the large later titanotheres, as in the chalicotheres, the entocuneiform is lost.

EQUOIDEA: The earliest equoid (*Hyracotherium*) had an entocuneiform similar to that seen in the early tapiroids. However, in the few specimens that I have been able to examine there was no evidence for either the presence or absence of metatarsal I. In view of the striking skeletal similarities between *Hyracotherium* and early Eocene tapiroids, it is probable that primitive equoids also preserved a vestige of the first metatarsal. In the cursorial Oligocene equoid *Mesohippus,* as in later horses, the entocuneiform is a flat, plate-like bone fused to the mesocuneiform, and the vestige of metatarsal I is lost.

DISCUSSION

The preceding brief survey suggests the following interpretations. A vestigial first metatarsal was present in the lightly built stem members of all five perissodactyl superfamilies, in which it served the same function as in modern tapirs—deep flexor attachment and tarsus brace. In the Equoidea, with increasing cursorial specialization and reduction of lateral digits, metatarsal I was lost, possibly because the contrahentes were no longer important for aid in the flexion of the lateral toes, or because metatarsal I was not needed for bracing the more compact tarsus. In titanotheres and chalicotheres, increase in body size resulted in a broadening of the tarsus and the reduction and loss of both metatarsal I and the entocuneiform, also seen in heavy tapiroids and rhinocerotoids, such as *Lophiodon* and *Teleoceras.* The loss of the entocuneiform and metatarsal I in these graviportal perissodactyls apparently reflects a structural adjustment of the tarsus to support increased

body weight, coupled with decreasing emphasis on speed and subsequently less need for the contrahentes and a tarsus brace. Also, the clawed chalicothere feet probably functioned in a manner unique to the Perissodactyla.

In running tapiroids and rhinocerotoids the pes remained tridactyl and a vestigial first metatarsal persisted. In rhinoceroses metatarsal I fused with the entocuneiform and, in the heavier forms, lost contact with metatarsal III, thus no longer bracing the tarsus. In tapiroids metatarsal I fused with the entocuneiform in only one cursorial end form (*Colodon*) but remained separate in all other genera up to the recent *Tapirus,* in which it serves for deep flexor muscle attachment and as a brace for the tarsus.

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